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Partial Mortality in *Porites* Corals: Variation among Philippine Reefs

key words: siltation, wave exposure, lesions, tissue necrosis, impact assessment, coral cover

Abstract

Partial mortality or tissue necrosis was quantified in the massive scleractinian coral *Porites* at three sites in The Philippines (Bolinao, NW Luzon; Puerto Galera, Mindoro; and El Nido, N Palawan). Overall, 15 ± 1 (mean ± 1 standard error, 642 replicates) percent of colony area was dead, mean colony area was 1135 ± 127 cm^2, and lesion density was 1.7 ± 0.1 dm^{-2}. Total live coral cover varied between 20 and 63% in belt transects, and *Porites* and *Acropora* cover were inversely correlated.

ANOVA models incorporating effects of site, colony size, sedimentation rates, wave exposure and depth were highly significant but explained only a small proportion of the variation observed in lesion density and percent dead area (respectively 8 and 2%). Lesion density was found to vary significantly with site (contributed 29% to this explained variance), decrease with increasing colony area (33%), and increase with increasing sedimentation (23%) and wave exposure (14%). Colony size was significantly explained by the factor site (contributing 61% to the total 29% explained variance) and depth (34%), with the smallest colonies being observed in Bolinao and the largest in El Nido. Densities of lesions were highest in Bolinao, intermediate in Puerto Galera, and lowest in El Nido. This pattern is parallel to intensity of human reef exploitation and opposite to that in colony size, live coral cover and *Acropora* cover. Since only a small part of the observed variance in partial mortality estimators was explained by the ANOVAs, other factors not quantified here must have been more important (e.g. disease incidence, predation, human exploitation).

1. Introduction

Reef-building corals are clonal organisms and partial mortality of colony tissue is a common phenomenon. Partial mortality or tissue necrosis (Riegl, 1995) involves the disappearance or retreat of living tissue from part(s) of the colony surface (called lesions) and may have many causes, ranging from diseases and predation to sediment scouring (Riegl, 1995; Meesters *et al.*, 1997; Lewis, 1997). Since lesions are often temporary injuries, their incidence as well as healing rates are considered good indicators for coral health (Jackson 1997; Van Woesik, 1998).

Heavy sedimentation has been associated with increased partial mortality (Hodgson, 1990; Rogers, 1990; Clarke *et al.*, 1993; Riegl, 1995; Nowlis *et al.*, 1997). The effect may be linked to increased silt loads either directly (e.g. scouring) or indirectly (increased turbidity reduces available energy; Meesters *et al.*, 1992). Increased sedimentation may have several other sublethal effects, such as reduction in recruitment rates (Rogers, 1990; Babcock and Davies, 1991; Wittenberg and Hunte, 1992), change in average colony size (Cortes and

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Risk, 1985; Rogers, 1990; Wittenberg and Hunte, 1992), reduced growth rates (Dodge *et al.*, 1974; Rogers, 1990) and increased metabolic demands (Riegl and Branch, 1995).

During several field campaigns, we quantified partial mortality in various ways for one particularly common coral taxon, the genus *Porites*, across a number of shallow coastal reefs in The Philippines, that we expected to span a range of sedimentation regimes around the reportedly critical threshold of 10 mg DW cm^{-2} d^{-1} of Rogers (1990). For the same coastal systems, Kamp-Nielsen *et al.* (in prep.) report that sediment silt and iron contents dropped rapidly whereas sand and calcium contents increased in a comparatively small transition zone. Hence, we have good evidence for the existence of non-linear siltation gradients and we expected this to be reflected in short-term sedimentation rates and coral partial mortality or cover as well. Additional to the more traditional scoring of coral growth form cover along transects, partial mortality would probably be responsive over shorter time scales and therefore be a potentially rapid assessment tool. Our goal was to establish whether partial mortality would be a clear function of sedimentation rates, so that it can function as a parameter in rapid assessment of reef status (sensu Risk, 1994; Maragos and Cook, 1995).

2. Materials and Methods

At three sites in the Philippines (Bolinao on Northern Luzon, Puerto Galera on Mindoro and El Nido on Palawan, Fig. 1), four to five stations (locations in Table 1) were selected along potential siltation gradients from river or creek mouths outward to the open sea. These same gradients have shown clear

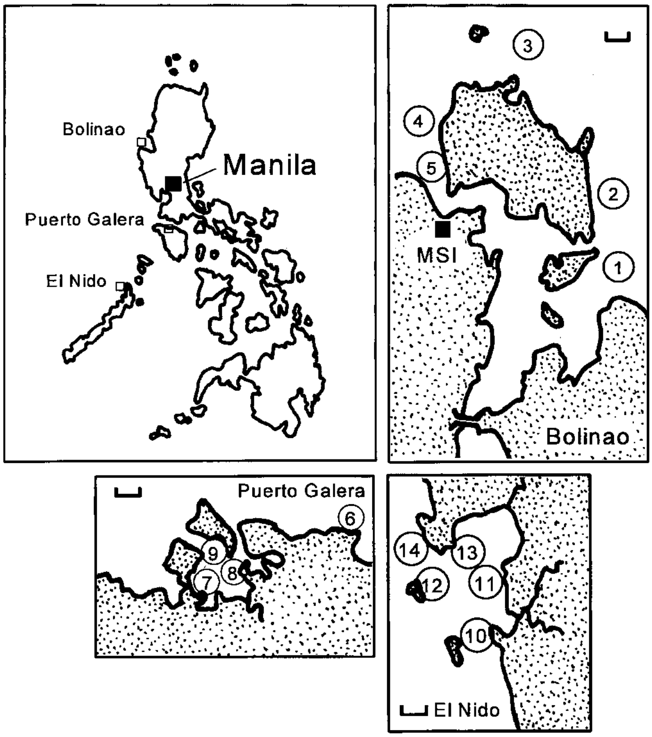

Figure 1. Location of the three study sites in the Philippines and position of the stations at these sites (detailed maps). Station numbers are conform those used in Table 3. In the Bolinao map MSI indicates the field laboratory of the Marine Sciences Institute. Scale bars indicate 1 km, North is top-of-page.

Table 1. Among-site comparison of short-term sedimentation rate, wave exposure, percent cover of live and dead coral, and percent cover of *Acropora* and *Porites*. Given are site means ± standard error (number of stations), the level of significance (p) of an among-site oneway ANOVA, and significant among-site differences from multiple comparisons (modified LSD-test maintaining an experimentwise error rate of 0.05, different letters indicate significantly different means). Sedimentation rates observed at separate stations are reported in Table 3.

Parameter	Bolinao	Puerto Galera	El Nido	p oneway ANOVA
sedimentation rate (mg DW cm^{-2} d^{-1})	18.3 ± 3.3 (4)	18.3 ± 1.5 (4)	17.5 ± 1.2 (5)	0.967
wave exposure (number of 45° compass sections)	b 5.2 ± 0.6 (5)	a 2.1 ± 1.0 (4)	b 5.6 ± 0.5 (5)	0.006
cover live hard corals (%)	a 26 ± 3 (5)	a 19 ± 7 (3)	b 52 ± 4 (4)	0.002
cover dead hard corals (%)	4 ± 3 (5)	5 ± 2 (3)	7 ± 1 (4)	0.532
cover *Acropora* (%)	a 3 ± 1 (5)	ab 6 ± 4 (3)	b 14 ± 5 (4)	0.068
cover *Porites* (%)	8 ± 4 (5)	6 ± 4 (3)	10 ± 6 (4)	0.823

decreases in abundance and species richness of seagrasses with increasing silt content of the sediment (Terrados *et al.*, 1998). A compromise had to be made between covering a range in silt loads and having sufficiently live coral cover. Where possible, existing data on water transparency and sedimentation rates were used to locate the stations (Hodgson, 1990; Rivera, 1997; MSI, unpublished). Data were collected during campaigns of about one week each, in May 1995, the onset of the rainy SW monsoon season.

At each of the stations, visibly comparable coral communities were sought that had at least 20% live coral cover and less than 40% sand cover at subtidal depths between 2 and 10 m. Within a station, a line was established parallel to the shore to maintain the selected depth, and in a 2 m wide section of 5–20 m length, all massive *Porites* colonies were measured until a total of 50 was reached. Also, cover of coral by growth form categories and other habitat characteristics were assessed according to English *et al.* (1994). In the Philippines, the genus *Porites* contains a number of species that are difficult to distinguish (Veron, 1986; Uychiaoco and Aliño, unpubl.), therefore, we refer here to the genus only. A colony was defined as any visibly separate coral skeleton with living tissue. Measurements involved total colony surface area, dead area and number of lesions. The total surface area or size (A, cm^2) of a colony was estimated by approximating it as a combination of a hemi-sphere and a cylinder, and applying the appropriate geometrical formula:

$$A = \pi * \sqrt{(L * W)} * H$$

where L is the maximum (horizontal) length of a colony, W is the maximum width perpendicular to the length, and H is the maximum height of the colony. In the case of plateform colonies, when colony height (H) was negligible, we used:

$$A = \pi * \left(\tfrac{1}{2} * \sqrt{(L * W)}\right)^2$$

To quantify the dead area on a colony, the size of each lesion was measured with help of a transparent plate on which squares of increasing area were drawn. Five lesion area classes were used: 0.1–1, 1–4, 4–16, 16–100 cm^2 and >100 cm^2. When a lesion was larger than 100 cm^2, its area was estimated as the number of times the 100 cm^2 – quadrat would fit in the lesion. The sum of all lesion areas divided by total colony area gave partial mortality (%).

At each station, three replicate sediment traps were placed vertically on the sediment and re-collected after approximately 24 hours. Traps had a diameter of 1.3 cm and a height of 6.25 cm, close to the width-depth criterion given by Gardner (1980) to prevent significant resuspension of trapped matter.

Upon return to the laboratory, the content of the traps was filtered off (Whatman GF/C), oven-dried (60 °C) for at least 48 hours and weighed (0.1 mg precision) to measure dry weight (DW). The comparatively short exposure times were a logistic necessity during the campaigns. Since time scales of lesion turn-over range between hours and months (MEESTERS *et al.*, 1992, 1997), we consider our 24 h exposure of traps acceptable. Duplicate sediment cores were taken from the transects and analysed for a number of parameters: grain size distribution (silt, fine sand and coarse sand, class limits 63 and 250 μm), water, organic matter, calcium and iron content as described in TERRADOS *et al.* (1998) and KAMP-NIELSEN (in prep.). In Puerto Galera, sediment cores were unfortunately not taken at the same stations as where coral parameters were quantified. A wave exposure index was estimated for each station from topographic maps as the number of 45° compass sections with open water for at least 2 km.

An overall ANOVA with four covariables (colony area, depth, wave exposure and sedimentation rate) and one fixed factor (sites) was used to detect overall patterns in partial mortality. Factor sums of squares were kept additive, so covariables were entered first and all variables were not entered simultaneously (NORUSIS, 1986). Oneway analyses of variance (ANOVA) and subsequent multiple comparisons (modified least significant difference test, maintaining an experimental error rate at 0.05) were carried out among stations within sites and subsequently among sites (using pooled data per site), to examine differences in sedimentation rate, colony size, partial mortality and number of lesions. Since the factor 'stations' can be seen as a nested factor within 'sites', these same data were also subjected to a nested ANOVA, largely leading to the same patterns as in the simple oneway ANOVA's. When necessary, $^{10}\log(x + 1)$ transformations were applied to homogenize the variances.

3. Results

Observed short-term sedimentation rates during the May 1995 campaign ranged between 10 and 30 mg DW cm^{-2} d^{-1} among stations, which is above the critical threshold of 10 mg DW cm^{-2} d^{-1} suggested by ROGERS (1990). Within the sites and among stations, however, no distinct gradients were observed in sedimentation rates, and also among the three sites no significant differences were found (Table 1). Wave exposure was substantially less in Puerto Galera (Table 1). Total live cover of hard corals as well as that of *Acropora* was significantly higher in El Nido than in the other two sites. Cover of *Acropora* and *Porites* were inversely related (Fig. 2a). Neither live coral cover nor *Porites* cover showed a significant relation with sediment silt content (Fig. 2b). Particularly live coral cover was highly variable among stations (Fig. 2b).

The overall ANOVA separating the effects of the factor site and four covariables on partial mortality (Table 2) suggests that important sources of variation were not addressed here,

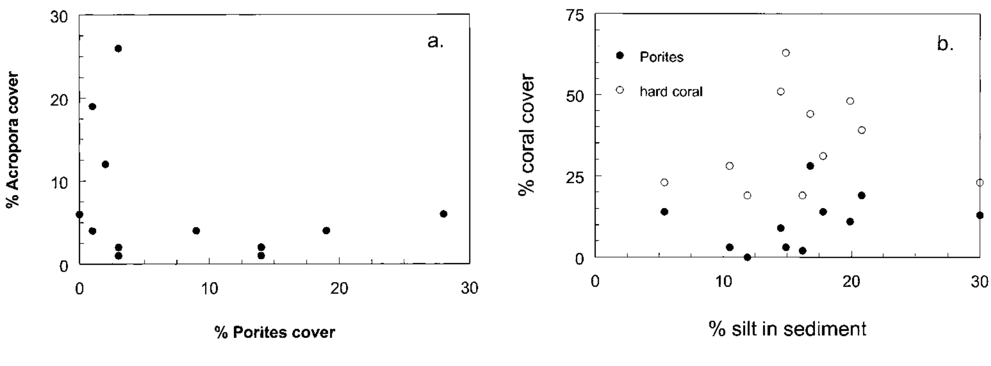

Figure 2. (a) Percentage cover of *Acropora* versus *Porites* in line transects at the sampling stations in Bolinao, Puerto Galera and El Nido. (b) Percentage live coral cover and percentage *Porites* cover as a function of sediment silt content.

Table 2. Analysis of variance for colony size, partial mortality and lesion density on *Porites* using site (Bolinao, El Nido and Puerto Galera) as fixed variable and total colony area, sedimentation rate, wave exposure and depth as co-variables. Covariables were entered first, sums of squares are additive. Given are the percentages of the explained variance due to the respective variables (%, calculated as variable sums of squares/total sums of squares explained by the model) and the levels of significance (p), as well as the percent of the total variation explained by the whole model (model sums of squares/total sums of squares) in the first column (ns = not significant, p > 0.05, then % explained variance not given).

Parameter	variation explained by the whole model	site		colony size		sedimentation		wave exposure		depth	
	%	%	p	%	p	%	p	%	p	%	p
total colony area	29	61	0.005	–		ns	0.531	ns	0.281	34	0.015
percentage partial mortality (% of total colony area)	2	ns	0.587	50	0.008	29	0.043	ns	0.093	ns	0.795
lesion density	8	29	0.001	33	0.001	23	0.001	14	0.010	ns	0.667

since the proportion of the total variance explained by the complete model was at best 29% for colony size, but much less for partial mortality and lesion density. Still, a considerable number of variables was highly significant for lesion density (Table 2).

The factor site (i.e. geographical variation) was responsible for a large part of the explained variance in lesion density and colony size (29 and 61%), and colony size was important for lesion density and partial mortality (33 and 50%). Lesion density declined significantly with increasing colony size, whilst partial mortality largely remained similar (Fig. 3). Hence, on larger colonies, the number of lesions was smaller, but lesions covered a similar proportion of the colony surface and thus were larger.

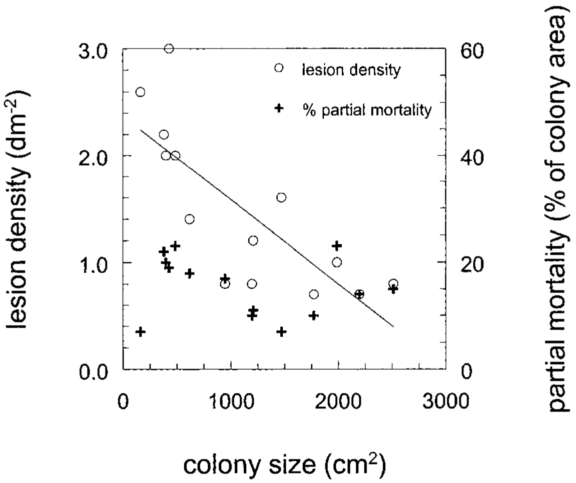

Figure 3. Lesion density and percent partial mortality as a function of *Porites* colony surface areas using station means from Bolinao, El Nido and Puerto Galera. The linear regression of lesion density versus colony size is significant ($p = 0.008$; $r^2 = 0.62$; intercept 2.37 ± 0.24, slope $-7.9 \times 10^{-4} \pm 1.8 \times 10^{-4}$).

Table 3. Observed short-term sedimentation rates (n = 3), colony size, percentage partial mortality (% dead colony area) per colony, and lesion density on *Porites* for all sampled stations at three sites in the Philippines. Data are presented as means ±1 standard error, the number of replicate colonies (n) is given in the last column. Levels of significance of oneway ANOVAs comparing coral parameters among areas and among stations within sites are given. All multiple comparisons were made after necessary log-transformation (modified LSD test, maintaining an experimentwise error rate at 0.05). Bold capitals accompanying the overall means depict significant differences among sites, lowercase italics depict significant differences between stations within a site. Station numbers are conform to those in Fig. 1. One excessively high sedimentation rate (station 4, indicated NC) has not been taken into consideration here.

site	station nr.	sedimentation rate (mg DW × cm^{-2} d^{-1})		colony size (cm^2)		partial mortality (%)		lesion density (n dm^{-2})	n
Bolinao	1	10.5 ± 1.3	*c*	1988 ± 624	*b*	23 ± 4		1.0 ± 0.3	26
	2	11.9 ± 1.0	*a*	162 ± 29	*a*	7 ± 2		2.6 ± 0.4	51
	3	20.8 ± 4.3	*b*	398 ± 78	*b*	20 ± 4		2.2 ± 0.4	50
	4	NC	*b*	380 ± 63	*b*	22 ± 4		2.0 ± 0.3	52
	5	30.0 ± 9.9	*a*	428 ± 132	*ab*	19 ± 3		3.1 ± 0.7	50
mean of site:			**A**	**528 ± 88**		**17 ± 2**	**B**	**2.3 ± 0.2**	**229**
oneway ANOVA among stations:				0.000		0.015		0.086	
Puerto Galera	6	17.8 ± 3.4		946 ± 202	*ab*	17 ± 2		0.9 ± 0.1	50
	7	16.2 ± 3.4		1470 ± 871	*a*	7 ± 2		1.6 ± 0.3	52
	8	19.2 ± 3.8		486 ± 104	*b*	23 ± 4		2.0 ± 0.3	51
	9	20.0 ± 2.3		2514 ± 671	*ab*	15 ± 3		2.2 ± 0.7	47
mean of site:			**B**	**1333 ± 282**		**16 ± 2**	**B**	**1.7 ± 0.2**	**200**
oneway ANOVA among stations				0.072		0.003		0.113	
El Nido	10	19.9 ± 2.5		618 ± 407		18 ± 4		1.2 ± 0.3	26
	11	16.8 ± 4.4		1772 ± 704		10 ± 3		1.3 ± 0.4	49
	12	14.5 ± 0.5		2198 ± 467		14 ± 4		0.8 ± 0.2	45
	13	21.4 ± 0.3		1196 ± 560		10 ± 2		0.8 ± 0.2	49
	14	14.9 ± 1.4		1208 ± 418		11 ± 3		0.8 ± 0.1	41
mean of site:			**B**	**1594 ± 251**		**12 ± 1**	**A**	**0.9 ± 0.1**	**213**
oneway ANOVA among stations				0.665		0.227		0.209	
oneway ANOVA among sites				0.001		0.043		0.001	

Note: nested ANOVAs testing for significance among stations within sites and among sites were carried out with these same data. Variation among stations within sites was allways significant ($p = 0.037$ or less). Variation among sites was not significant for partial mortality only ($p = 0.060$), but highly significant for the two others ($p < 0.001$).

The importance of geographic variation is largely confirmed by the comparisons of overall site means (Table 3): on average, colonies in Bolinao were significantly smaller than at the other sites, and lesion density was higher. *Porites* colonies at Puerto Galera were as large as those of El Nido, but lesion density was similar to that of Bolinao. Among station differences within a site were often significant, particularly in Bolinao (Table 3). Nested ANOVAs confirmed the significance patterns from the oneway ANOVAs by-and-large, with the exception of the effect of stations within sites on the % partial mortality that was almost significant only ($p = 0.06$).

The covariable sedimentation did affect the percentage partial mortality (Table 2, $p = 0.043$) and lesion density (Table 2, $p = 0.001$). Lesion density increased with both increasing sedimentation and wave exposure, since both were significant ($p < 0.01$) and had positive slopes in a stepwise multiple regression of residuals from the linear regression of lesion density with colony size, i.e. after removal of the large colony size effect. The covariable wave exposure only affected lesion density significantly (Table 2).

4. Discussion

Differences in lesion density found among the three sites were considerable, but variation among stations within a site were equally large. In two of the three sites, a distinct, nonlinear, siltation gradient was observed (i.e. Bolinao and El Nido, but not in Puerto Galera, based on the sediment core data in KAMP-NIELSEN *et al.*, in prep.; note that for Puerto Galera the stations for sediment cores and coral did not match). However, the short-term sedimentation rate we quantified with traps, as well as wave exposure and depth could only explain a limited, though significant, part (2–8%) of the total observed variance in lesion density or percent partial mortality. So other factors not quantified here, or random variation, must have been more important.

On average, El Nido had larger colonies with less lesions than those in Bolinao. Puerto Galera was intermediate, with larger colonies but also higher numbers of lesions. Also total live coral cover and cover of *Acropora* was higher in El Nido. This pattern can only be explained by factors outside the presently collected data-set. We were unable to identify sufficiently quantitative data sources for biological causes of partial mortality at our three sites, but a substantial difference in the degree of human reef exploitation is qualitatively apparent: the coastal waters off Bolinao, Puerto Galera and El Nido form a gradient of decreasing human exploitation including fishing pressure, deforestation and unsustainable land use (UNEP/IUCN, 1988; HODGSON, 1990; MCMANUS and CHUA THIA-ENG, 1990; KUMMER, 1991), whilst the remote El Nido on Palawan has only recently been exposed to larger scale deforestation (HODGSON, 1990; KUMMER, 1991). The general decrease in coral cover and *Porites* colony size and the increase in lesion density on *Porites* along this gradient suggests a human exploitation-linked deterioration in coral performance. Several confounding factors, however, may play a role (e.g. variation in fish fauna, disease incidence, lesion recovery capacity in the corals; MEESTERS *et al.*, 1992, 1997; VAN WOESIK, 1998). In a similar way, LEWIS (1997) was unable to find a linear pattern in partial mortality in *Siderastrea siderea* along a eutrophication gradient on Barbados reefs.

Few reports give quantitative estimates of partial mortality in scleractinian corals and all are from the Caribbean. With the exception of the high values reported by LEWIS (1997: 38–49% for *Siderastrea siderea*), existing estimates remain below 5% of the colony surface (MEESTERS *et al.*, 1996 and 1997: 1–3% for various taxa including *Porites;* RIEGL, 1995: <1%). WESSELING *et al.* (1999) reported up to 45% partial mortality for Philippine *Porites* after 68 hours of full colony burial, but substantial recovery was observed in subsequent weeks. LEWIS (1997) qualified his Barbados reefs as degrading, but it is difficult to pinpoint the cause of his high values of partial mortality. Our observed range (overall mean was $15 \pm 1\%$) is lower than the one found by LEWIS (1997), or the one induced by WESSELING *et al.* (1999), but considerably less than that observed by MEESTERS *et al.* (1996, 1997) for Carribean coral taxa (including *Porites*) that were probably little affected by sedimentation.

In short, we found considerable partial mortality in shallow water *Porites* in The Phillipines and could explain observed variation only partially by differences in sedimentation, wave exposure, colony size and a site effect that is probably related to human exploitation. However, since our model only explained a limited part of the observed variation, other factors must be important as well. Also, we therefore probably have to reject partial mortality or lesion density on *Porites* as a suitable parameter for rapid appraisal surveys.

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